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Anthropogenic Disturbances Shape Soil Capillary and Saturated Water Retention Indirectly via Plant Functional Traits and Soil Organic Carbon in Temperate Forests

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Abstract: Soil's water-physical properties support essential soil water retention functions for driving water distribution and availability, which is vital for plant growth and biogeochemical cycling. However, the question concerning how tree compositions and their interactions with other abiotic factors modulate soil's water-physical properties in disturbed forests remains poorly understood. Based on observational data from nine permanent forest sites (18,747 trees and 210 plots) in the northeast of China, where forests once undergone three different levels of anthropogenic logging disturbance, we evaluated how multiple biotic (i.e., tree diversity and functional trait composition) and abiotic (soil texture and soil organic carbon) factors influence water-physical properties (i.e., in terms of soil capillary water retention (WC) and soil saturated water retention (WS)) in temperate forests. We found that the impacts of logging disturbance on soil water-physical properties were associated with improved tree diversity, acquisitive functional traits, and SOC. These associated attributes were also positively related to WC and WS, while there was no significant effect from soil texture. Moreover, disturbance indirectly affected soil water-physical properties mainly by functional traits and SOC, as acquisitive functional traits significantly mediate the effect from disturbance on WC and SOC mediates the influence from disturbance on WS. Finally, our results emphasize the potential relationships of tree composition with SOC and soil water retention as compared with soil texture and hence suggest that plants can actively modulate their abiotic contexts after disturbance, which is meaningful for understanding forest health and resistance.

Keywords: biodiversity; ecosystem functions; logging disturbance; plant functional traits; soil water-physical properties

1. Introduction

Soil water-physical properties support essential soil water functions (such as soil capillary water retention and soil saturated water retention) which could potentially affect biogeochemical cycling and alleviate the negative effect of hydrological variations [1]. Typically, researchers have focused on the influence of soil textures and soil organic carbon content (SOC) on soil water-physical properties [2–5]. However, in recent studies, researchers have highlighted the diversity influence such as improved biomass and SOC or the presence of particular functional groups on soil water infiltration in the grassland ecosystem [6,7]. Thus, we have acknowledged that both plant composition (such as tree diversity and functional trait composition) and soil attributes (such as soil texture and SOC) are essential to understanding soil water-physical properties. However, how soil water retention is related to these multiple biotic and abiotic factors remains poorly explored, especially in natural forests under the increasing human interference.

Soil texture and SOC are the two basic factors influencing soil water-physical properties. For example, soil water characteristics can be evaluated by these soil data using pedotransfer functions [8,9], even though their relative importance could vary under different circumstances [2,4]. Rawls et al. [10] have reported that the relationship between soil texture and soil water-physical properties changed with various SOC content in soils. Moreover, some studies have found that the input of different organic matter in soil could form various soil pore systems and soil aggregates due to soil microbial activities [11]. Finally, given the plant manipulation on soil texture and SOC [12,13], these studies lead us to expect the effect of tree composition on soil water retention.

Plant community could affect soil texture, SOC, and soil water-physical properties via multiple interacting pathways. For instance, plants in the community with high diversity and different niches could absorb more resources, facilitating the community to possess greater above- and below-ground biomass, and thereby increase SOC contents [14] and other associated soil properties. The experimental studies have shown that species diversity could improve soil infiltration via increased soil porosity and SOC [15]. A similar trend is evident for a natural chronosequence of grassland [6]. On the other hand, dominant plant species in a community often show an essential influence on ecosystem functions due to associated functional trait composition [16]. For instance, Dawud et al. [17] have reported that tree species functional group, litterfall quality per se, and its decomposing rate rather than the diverse or the amount of litterfall input better explained the variance of SOC content. Moreover, the qualitative difference of litterfall could induce different aggregations of silt-associated (>53 μm) and clay-associated (<53 μm) organic matter fraction in soil [18,19], which influences the dispersion of soil porosity and structure. Also, Teixeira et al. [20] have reported that the community trait composition of specific leaf area could explain more variance of water retention capacity than other predictors in semi-arid forest ecosystems. Taken together, the above viewpoints link to two prominent theories (i.e., niche complementarity and mass ratio mechanisms [21,22]), which provide the quantitative relationship between biodiversity and ecosystem functions.

Under global change circumstances, forest ecosystems usually changed with a variety of human activities, and logging disturbance is a common disturbance for timber use in forests [23]. These logging disturbances lead to alterations of tree composition, above- and below-ground functions [24,25], and biogeochemical processes [26]. During the recovery process, tree composition often shows great importance to drive multiple ecosystem functions and processes [27]. For example, functional traits composition in the community can reflect the resource status of the environment while plants are alive and the ability to modulate their abiotic contexts after death [27]. The acquisitive functional traits (e.g., high leaf nitrogen content, specific leaf area) are often related to the fast-growing community and produce easily decomposed litterfalls that benefit biogeochemical cycles [28,29]. Moreover, plant diversity has usually related to increased production, and diverse litterfall inputs could enhance decomposed processes due to complementarity effects [30,31]. As such, given the importance of soil water-physical properties in regulating soil water content and ecological processes, how soil water retention reacts to disturbance and how it relates to tree composition are crucial for understanding forests resilience and processes recovering from disturbances [32].

This study aims to explore how multiple biotic (i.e., functional trait composition and diversity) and abiotic (soil texture and soil organic carbon) factors drive soil water-physical properties (i.e., in terms of capillary water retention (WC)), and soil saturated water retention (WS), in temperate forests recovering from different logging disturbance intensity levels. Here, we mainly focus on two types of soil water-physical properties due to their relations with soil water availability for plant growth and reducing surface runoff and soil erosion [33]. To do this, we use detailed tree and soil data from nine permanent forest sites (in total 210 subplots) on Changbai Mountain in the northeast of China where forests underwent historic anthropogenic logging disturbance. We aim to answer the following main research questions: (1) How do soil water-physical properties and associated drivers vary with disturbance intensity? (2) How does disturbance affect soil water-physical properties directly, and indirectly via tree diversity, functional trait composition, and SOC? (3) What are the implications for recovering processes from the alteration of soil water-physical properties and plant attributes after disturbance?

2. Materials and Methods

2.1. Study Sites and Forest Inventories

Our study area is located in the northeast of China, covering the Liaoning and Jilin Provinces (Figure 1, Table S1), which is classified as a temperate continental climate. The mean annual air temperature is 2.8 °C, and the coldest and warmest monthly means are −13.7 °C in January and 19.7 °C in July, respectively [34]. The mean annual precipitation is 700 mm, which mostly occurs during the growing seasons (from June to September). Broad-leaved Korean pine (*Pinus koraiensis* Sieb.et Zucc.) mixed forest, well-known for its high species diversity, productivity and complex stand structure, is the dominant vegetation type in the study region. The predominant soil type of the studied area is Alfisol according to the US soil taxonomy [35]. Moreover, some areas in this region had been subjected to variable intensities of human disturbances, but there were no severe human disturbances since 1998 when the forest protection policy was strictly implemented [36].

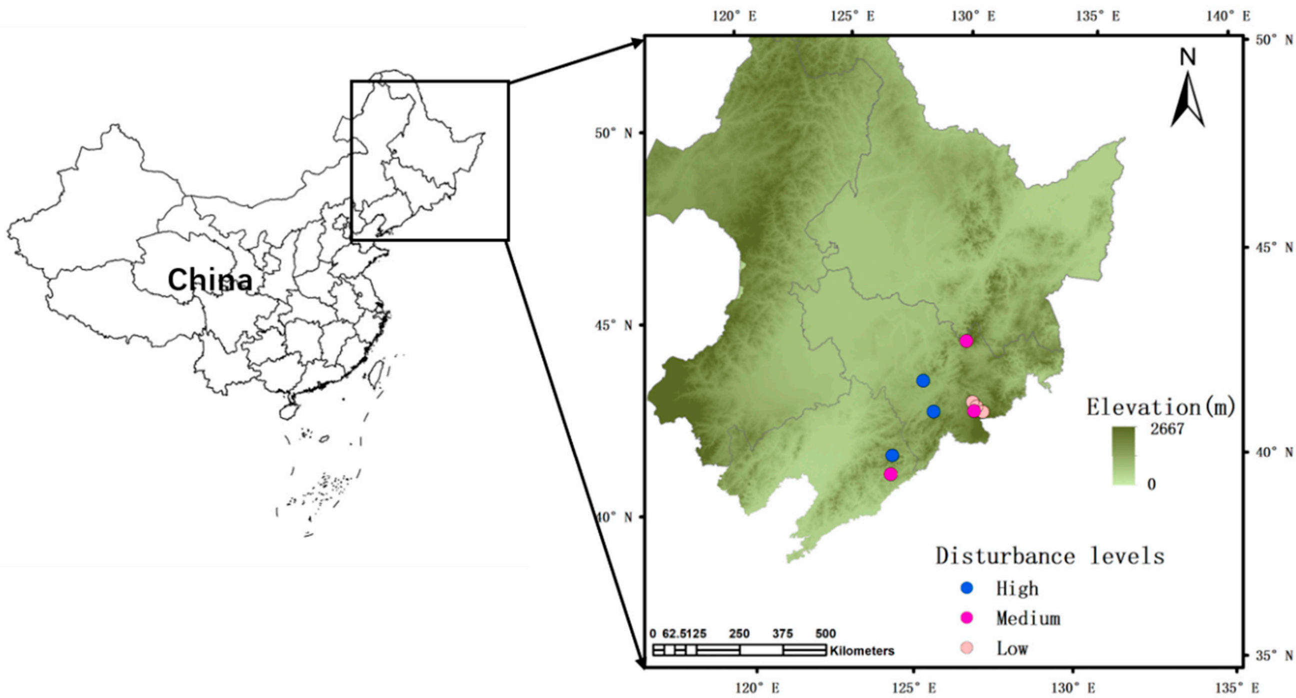

Figure 1. Map of China showing the study area and distribution of forest sites. The colors of dots represent disturbance levels at each site.

To quantify the relationship between plant biodiversity and ecosystem functions under varied logging disturbances in the previous studies, permanent forest sites were established over the district [25]. Here, we selected nine sites (0.6–1 ha) to research the diversity relationship with soil water retention function. Within each site, all trees with a diameter at breast height (DBH) > 1 cm were marked, measured, recognized to species level, and positioned in contiguous 20 m × 20 m subplots [34]. In total, our data covered

18,747 stems in total belonging to 81 species, 46 genera, and 26 families across 210 subplots. In addition, the topography of each subplot was measured by assessing the elevation of four corners in each subplot using an electronic distance measuring device and then the mean elevation, and the slope was calculated for each subplot according to the method used in Harms et al. [37]. The elevation of the studied plots ranged from 640.4 to 1023.1 m.

2.2. Assessment of Disturbance Intensities

The disturbance intensity of each site was assessed by counting the number of removed tree stumps by a chainsaw [38], and anthropogenic activities were prohibited since 1998 due to the implementation of the Nature Forest Protection Project [36]. Additionally, the official records of the Local Forestry Bureau in Jilin and Liaoning Provinces were checked to collect the relevant selective logging data. Collectively, plots were primarily classified into three disturbance intensity levels according to the partial harvesting (e.g., thinning, selective harvesting): relatively low (<10%), medium (10–20%), and high (20~30%) disturbance. Plots with medium and high disturbance levels were primarily located around the residential area, whereas plots with low disturbance levels were located in the main region of the Changbai Mountain Nature Reserve (Figure 1), which was established in the 1960s and is part of the World Biosphere Reserve Network under the Man and the Biosphere Project in 1980 [39].

2.3. Quantification of Plant Functional Trait Compositions and Diversity Attributes

Community-weighted mean (CWM) of functional trait values and functional diversity (functional dispersion) were calculated by five functional traits which were closely associated with forest growth, recruitment, and death [40], including maximum height (MH), leaf area (LA), specific leaf area (SLA), leaf nitrogen content (LNC), and leaf phosphorus content (LPC). The detailed measurement approaches for these five functional traits are described in Yuan et al. [41]. The community weighted means of each trait (CWM.H, CWM.LNC, CWM.LPC, CWM.LA, and CWM.SLA) within each plot were weighted by the species' relative basal area [42]. Both functional dispersion and CWM of functional traits were calculated by FD package in R 4.0.2 [43]. Besides, plant diversity indices such as species richness (S) and Shannon-Wiener diversity (H) were calculated for each subplot.

2.4. Quantification of Soil Basic Properties and Soil Water-Physical Properties

In 2018, we randomly selected three soil sampling sites in the midpoints between the central point and four corners in each 20 m × 20 m subplot. In each sampling site, after removing large debris, soil corers using stainless cylinders of 100 cm^3 in volume were selected for the bulk soil density and soil capillary porosity measurement. The corers containing large roots were abandoned for the precise analyses of data. Subsequently, five soil cores (3.8 cm in diameter, 10 cm deep) at each sampling point were collected, pooled, and transferred to the laboratory with plastic zipper bags for further chemical analyses. Soil organic carbon analysis was measured by the dichromate oxidation method [44], and soil particle size was determined by laser diffraction using a Mastersizer 2000 Particle Analyzer.

Soil water retention was measured through soil porosity, which could be divided into capillary porosity, and total porosity corresponding to soil capillary water retention (WC), and soil saturated water retention (WS) [33].

The soil capillary porosity (%) (CP) was measured as CP = $(W/V) \times 100$, where W was measured by the weight difference of moist and dry soil cores, and moist soil core was the weight after placing the stainless cylinders soil core in a tray with a 5-mm level of water until filter paper at the top of each core became moist according to Liu, Zhang, Heathman, Wang and Huang [12], V is the volume of the soil core (cm^3). The total soil porosity (%) was measured as TP = $(1 - \mathrm{BD/ds}) \times 100$, where BD is the soil bulk density (g cm^{-3}), and ds is the soil particle density (2.65 g cm^{-3}).

Finally, soil water retention was calculated as WC = 10,000 × CP × *h*, and WS = 10000 × TP × *h*, where *h* was the soil depth, and for more accuracy, we only evaluated the top 0.1 m of the soil layer.

2.5. Statistical Analyses

Firstly, we assessed the effects of disturbance on soil water-physical properties (WC and WS) as well as the related above- and below-ground attributes using one-way ANOVA analysis, and Post-hoc Tukey's test was conducted to assess the significant difference among disturbance levels. Then, we conducted correlation analyses (Spearman's) for soil water retention and all related indicators for the basic understanding of the relationship between them. For the clear presentation of variations of attributes among disturbance levels, the principal component analysis (PCA) was also performed over soil water retention and all indicators considering three disturbance levels.

Finally, we used a piecewise structural model (pSEM) to evaluate how disturbance influence soil water-physical properties directly and indirectly [45]. We choose sites as the random effect. As to reduce the multicollinearity, we also conducted a PCA analysis on five functional traits, and then, used PCA1 (CWM.pca1) in the pSEM analysis to represent community functional traits. We found the CWM.pca1 (high CWM.LA, CWM.SLA, CWM.LNC, CWM.LPC, and low CWM.H) explained 75% of the total variance of all functional traits which could represent the acquisitive functional strategy along the leaf economic spectrum [29]. We used Fisher's C statistics ($p > 0.05$) to check the model fit [46]. The conditional ($R^2{}_c$) and marginal ($R^2{}_m$) R^2 were calculated for each of the dependent variables [47].

All predictors, except disturbance levels (i.e., ordinal grouping variable), were standardized to a mean of 0 and a standard deviation of 1, whereas the response factors (WC and WS) were natural-log transformed before standardization. All analyses were conducted in R. 4.0.2 (Team RDC, 2019).

3. Results

The mean soil capillary water retention (WC) and soil saturated water retention (WS) in the study area were about 553 and 796 t hm^{-2}, respectively (Table S2). The SOC content was 148 g kg^{-1} on average, and the relative proportion of clay, silt, fine sand, and sand texture was 34.2%, 34.0%, 28.4% and 3.3%, respectively. The mean species richness (S) was 15 with ranging from 7 to 29, while the community-weighted mean of specific leaf area (CWM.SLA) varied widely from 113.0 to 522.5 cm^2 g^{-1} with a mean of 234.7 cm^2 g^{-1} (Table S2). Disturbance significantly changed plant composition, SOC, and soil water-physical properties (Figure 2). WC and WS were significantly greater at the high disturbance level, whereas SOC content significantly increased along with three disturbance levels. Tree compositions, such as tree diversity (S, H, FDis) and community-weighted mean of leaf traits (e.g., CWM.SLA, CWM.LA, CWM.LNC, and CWM.LPC) in highly disturbed plots were significantly greater than those in low disturbed plots, and CWM.H was lower than those in low disturbed plots (Figure 2). In accordance with functional trait composition, low disturbed forests were dominated by *Pinus koraiensis* Sieb.et Zucc., *Tilia amurensis* Rupr., *Larix gmelinii* (Rupr.) Kuzen., and *Acer pictum subsp. momo* (Maxim.) H. Ohashi where highly disturbed forests were mainly dominated by *Pinus koraiensis*, *Juglans mandshurica* Maxim., *Abies holophylla* Maxim., *Carpinus cordata Bl.*, and *Prunus maackii* Rupr.(Table S1).

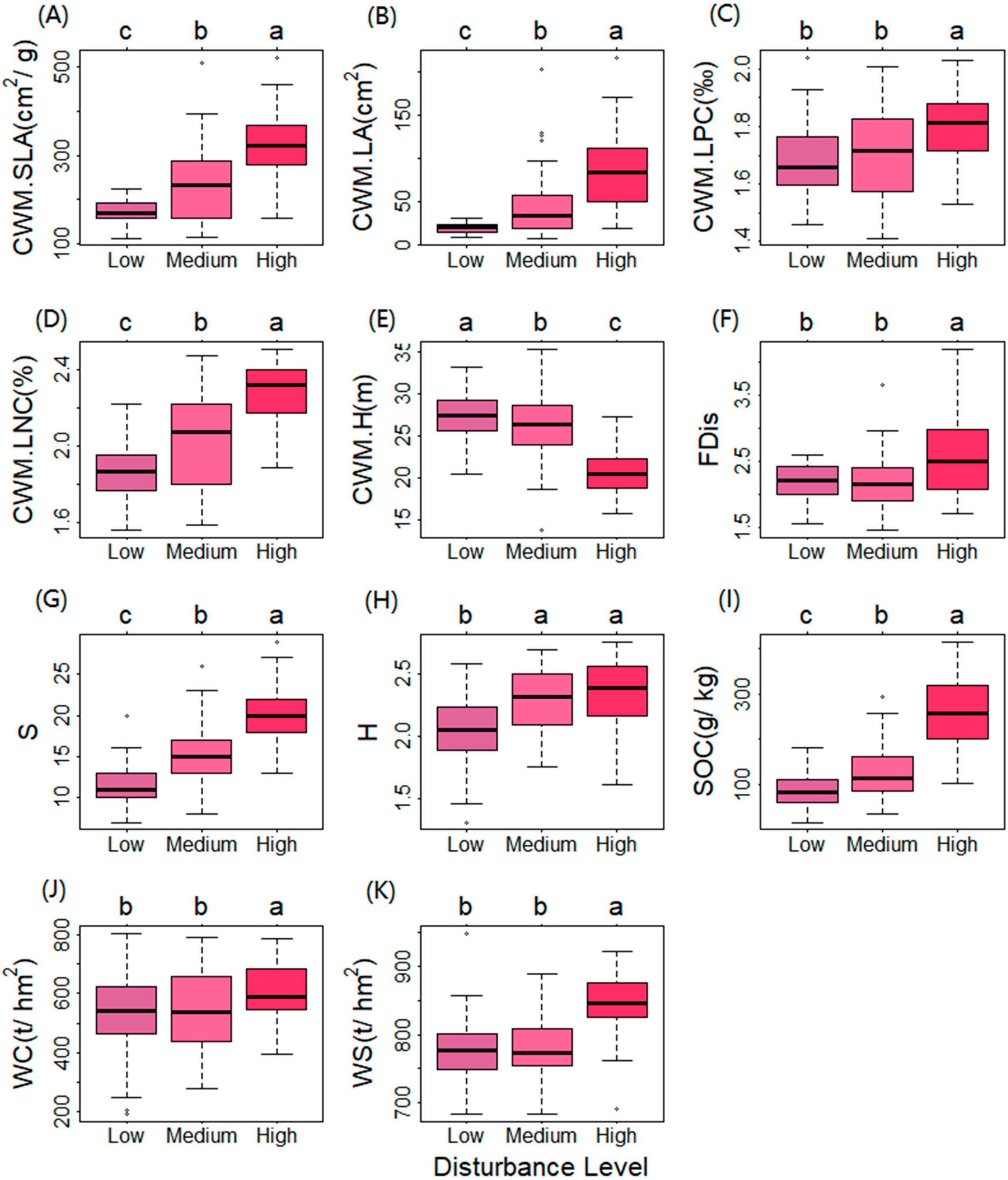

Figure 2. The influence of disturbance intensity on (**A**) community weighted mean of specific leaf area (CWM.SLA), (**B**) community weighted mean of leaf area (CWM.LA), (**C**) community weighted mean of leaf phosphorus content (CWM.LPC), (**D**) community weighted mean of leaf nitrogen content (CWM.LNC), (**E**) community weighted mean of maximum tree height (CWM.H), (**F**) tree functional dispersion diversity (FDis), (**G**) tree species richness (S), (**H**) tree Shannon diversity (H), (**I**) soil organic carbon content (SOC), (**J**) soil capillary water retention (WC), and (**K**)soil saturated water retention (WS). Different letters (a–c) reflect significant (Tukey's test, $p < 0.05$) differences between three different disturbance levels. Boxplots represent median, first and third quartiles, and upper hinge and lower hinge. Abbreviations are same as below.

After different levels of disturbance, there were coordinated and significant alterations of soil water-physical properties and related factors. The correlation analyses showed that FDis and soil texture were basically uncorrelated with WC, WS, and most other factors, whereas the remaining factors are significantly associated (Figure S1). PCA analyses among these factors presented two clear dimensions of factor variation standing out over the plane, where PCA1 and PCA2 explained 61% of the total variance (Figure 3). One-dimension PCA1 was related to functional traits, tree diversity, SOC, WC, and WS, and the other dimension PCA2 mainly related to soil texture. PCA1 appeared with a clear continuum of functional traits that changed from conservative functional traits (CWM.H) to acquisitive functional traits (CWM.SLA, CWM.LA, CWM.LNC, and CWM.LPC) along the disturbance gradients. This continuum was to the accompaniment of greater tree diversity, SOC, WC, and WS. Collectively, highly disturbed plots were in the cluster at the end of acquisitive functional traits, with greater tree diversity, SOC, WC, and WS, and low disturbance plots were grouped at the other direction end, whereas the middle disturbance plots were spread in-between these two directions.

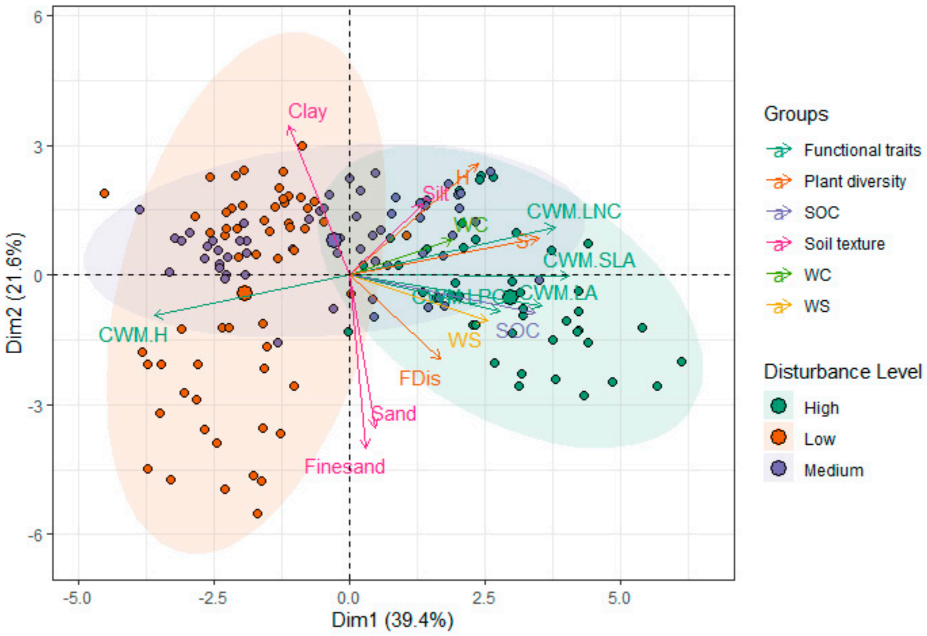

Figure 3. The principal component analysis (PCA) of soil water retention and all predictors. PC1 and PC2 explain 61% of the total variance. Circles of different colors mean three disturbance levels.

The pSEM results revealed how disturbance influence WC and WS indirectly and directly through related factors such as the community-weighted mean of functional traits, tree diversity, and SOC (Figure 4a,b). Results showed that disturbance improved WC and WS mainly through functional traits and SOC while there is no direct influence from logging disturbance. Specifically, acquisitive functional traits (CWM.pca1, increased CWM.LA, CWM.SLA, CWM.LNC, CWM.LPC, and lower CWM.H, Table S4) increased with disturbance intensity and thereby improved WC while SOC also increased with disturbance and then improved WS. However, in contrast to functional traits composition, plant diversity did not impact WC and WS (Figure 4a,b).

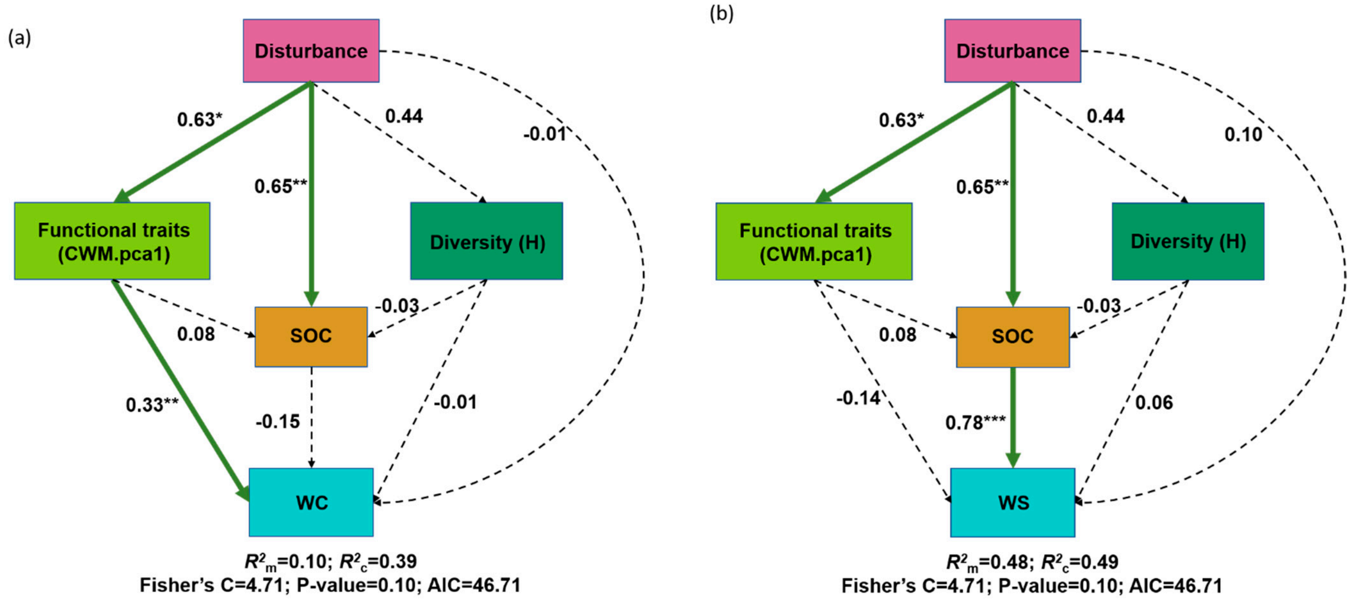

Figure 4. Pathways showing how logging disturbance affects WC (**a**) and WS (**b**) based on piece-wise structural equation models (pSEMs). Numbers adjacent to arrows represent the effect size of the relationship. Continuous arrows indicate significant pathways whereas dashed arrows indicate insignificant pathways. The significance of relationships was also given (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

4. Discussion

In this study, we elucidate the coordinated alteration of soil water-physical properties with plant attributes and SOC after disturbance and tease apart how disturbance affects soil water retention via plant attributes and SOC. We will discuss the results in the following points: (1) shifts of the plant community composition and soil water retention after disturbance; (2) disturbance increases soil water retention via SOC and functional traits and mainly through indirect ways; (3) what is the implication to recovering processes as coordinated alterations of soil water retention with plant attributes.

The improved WC and WS, along with the increasing disturbance intensity, are highly associated with the alteration of multiple plant attributes (increased acquisitive traits composition and diversity), while soil texture showed no relation with WC and WS (Figure 3 and Figure S1). This result highlights the importance of biotic factors in regulating soil water-physical properties. Specifically, multiple tree diversity indices (H and S) have increased under high disturbance levels, consistent with most previous findings in temperate and boreal forests [48]. This phenomenon follows the fact that past logging activities have decreased numbers of large trees which in turn creates forest gaps, and hence, more saplings or colonizing seedlings emerge due to greater light resources [49]. Accordingly, communities were dominated by acquisitive traits (CWM.SLA, CWM.LA, CWM.LNC, and CWM.LPC) along disturbance gradients, coupling with more fast-growing species under more light resources [27]. As such, soil water retention and SOC have changed along with the shift of the plant community. However, disturbance intensity and recovery time are critical for the trajectory of recovery of plant community attributes and ecosystem functions [26,50]. In our research, the initial logging activities (prohibited after 1998) might have caused compaction in soil and consequently affect soil water-physical properties. Nevertheless, this compaction effect could disappear after 10 years of recovery [51], which is in line with our results that there are only indirect pathways about how disturbance influence WC and WS (Figure 4).

Although positive associations of WS and WC with SOC, tree diversity, and acquisitive functional traits, disturbance drives soil water retention mainly through SOC and functional traits (Figure 4). SOC as the consequence of litter decomposition and microbe activities, varying in amounts and composition due to the complex interactions of litterfall input and soil texture, usually show essential mediator effects on soil structure [4,52]. For example, studies have highlighted that SOC as the response to increased species diversity performs a key role in regulating soil infiltration capacity in experimental and natural grasslands [6,15]. Consistent with these grassland cases, we found SOC is the primary factor influencing WS in disturbed forests associating with greater tree diversity despite the insignificant pathway in pSEM. In fact, the initial logging disturbance has produced large amounts of detritus left in the soil and this may also explain the trend of increased SOC with increased disturbance intensity [53]. This fact may explain insignificant pathways from functional traits composition and diversity to SOC compared to significant influence from disturbance to SOC (Figure 4). Thus, the increased SOC increased WS by reducing soil bulk density and increasing soil porosity [4]. In contrast, acquisitive functional traits are key factors influencing WC, while previous results have shown forest types with easily decomposed litterfalls often accompanied by high WC [54,55]. This result might be due to the reason that acquisitive functional traits generally relate to labile decomposing litterfalls, which could be beneficial to the formation of mineral-stabilized soil organic carbon [56,57] and soil aggregates [58], thereby increasing WC. Furthermore, the significance of functional traits rather than the increased diversity in regulating WC, confirms the mass-ratio theory in explaining the relationship between WC and tree composition. However, the mass-ratio and niche-complementary theory are not incompatible, and how diversity effect and functional trait composition influence soil physical properties remain poorly explored, which needs more focus in the future [59].

There is a coordinated improvement of tree diversity (e.g., FDis, H, and S), acquisitive functional traits, SOC, WC, and WS in high disturbed forests. Similarly, we also found that soil fertility in highly disturbed forests was better than in low disturbed forests (Table S3). These coordinated alterations claim the ecological linkages between plant attributes and soil water retention according to ecosystem processes [60]. For example, the increased plant diversity and acquisitive functional trait composition can enhance biogeochemical cycling via increased rates of litterfall decomposition, soil nutrient availability, and soil water retention [27,28,60]. In reverse, high soil water retention and infiltration capacity imply a better soil moisture condition [3,61] which means better habitats and benefit higher plant diversity and net biome productivity [62,63]. In this sense, rather than the view focusing on the link of plant diversity effect and nutrient availability, the positive relationships between tree diversity, acquisitive functional traits, and soil water-physical properties strengthen these biochemical cycles from the perspective of water resources [27]. Thus, these positive interactions of plant composition and soil water retention provide an integrative understanding of how ecosystem processes change with anthropogenic disturbance.

Our research demonstrates that soil texture shows no relation with WC and WS, whereas functional traits and SOC have a profound impact on soil water-physical properties (Figure 3). Soil texture also shows no influence on soil water-physical properties across various circumstances [4,15,64], and the reason for this may be their low contributions when compared with other factors. Moreover, it is worth noting that there are other drivers affecting soil hydraulic properties crucially, such as root system and earthworm activities [65,66], although we barely mentioned them in this research. As such, soil structure is the consequence of multiple interactions of plant attributes and ecosystem processes, which underscores the necessity of an integrative understanding of biotic and abiotic drivers influencing soil water-physical properties.

5. Conclusions

By explicitly considering plant functional traits, diversity, SOC, and soil texture related to anthropogenic disturbance and soil water-physical properties, we found that disturbance intensity has significant and indirect effects on soil water-physical properties. The indirect effects on soil water-physical properties mainly come from disturbance induced changes in functional traits composition and SOC, as disturbance positively improves WC via increased acquisitive functional traits and improves WS via increased SOC, respectively. These different pathways affecting WC and WS show different mechanisms determining WC, WS, and the complexity of soil structure and its interactions with plant composition. Moreover, the coordinated transformation of acquisitive functional traits and tree diversity with soil water retention, highlights the importance of plant attributes in modulating soil water-physical properties and suggests altered biogeochemical patterns in communities after disturbance. Together, our results provide insight into the response of plants attributes and their abiotic contexts to anthropogenic disturbance, enabling an integrative understanding of forest recovery after disturbance which is meaningful to forest management.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/f12111588/s1, Table S1: The descriptive summary of the studied sites and plots, Table S2: The descriptive statistical summary of soil functions and plant attributes, Table S3: Soil nutrient content among different disturbance levels and their difference based on one-way ANOVA analysis, Table S4: The standardized loadings of CWM.pca1 on functional traits based on principal component analysis, Figure S1: Spearman's correlation relationship between soil water retention and community attributes. Red to blue color indicates negative to positive correlations, and the numbers inside the square represent correlation coefficient (r). Crosses inside the circles indicate insignificant ($p > 0.05$) correlations.

Author Contributions: S.L.: conceptualization, methodology, formal analysis, writing-original draft, writing-review and editing. Z.Y.: conceptualization, methodology, writing-review and editing, supervision. A.A.: conceptualization, writing-review and editing. A.S.: conceptualization, writing-review and editing. Z.M.: writing-review and editing. F.D.: investigation. D.Z.: investigation. S.F.: investigation. Z.J.: investigation. Z.T.: investigation. F.L.: investigation. J.Y.: investigation. X.W.: conceptualization. Z.H.: conceptualization, investigation, supervision. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: Dataset and associated R codes used in the main results are available upon reasonable request to the corresponding author.

Conflicts of Interest: The authors declare no competing financial interests.

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